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OBSERVATIONS ON THE INNERVATION OF THE SUBLINGUAL AND SUBMAXILLARY GLANDS

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Plate XI.

In a research published by Retzius[1] in 1880, which gives the detailed results of an examination of the various ganglia found in connection with many of the cerebral nerves, the jugular and cervical ganglia of the vagus, the jugular and petrosal of the glosso-pharyngeal, the geniculate of the seventh and the Gasserian of the fifth, are described as presenting a structure identical with that of the spinal ganglia. The acoustic ganglion, while it presents some structural peculiarities, was also classed with this group. All other head ganglia—namely, the otic, spheno-palatine, ciliary, and submaxillary—are described as containing cells resembling those of the sympathetic system. The above observations were made on teased preparations, which no doubt accounts for the fact that they did not receive the general recognition due them.

Thanks to the Golgi method, doubts concerning the shape of a nerve cell need no longer be entertained. This method has shown that cells of the spinal ganglia possess a round or oval body, from which springs a single process which divides into two branches a short distance from the cell body, while the sympathetic cells are multipolar, having one axis-cylinder process and numerous protoplasmic branches. The two types are not to be mistaken.

Accordingly we find that nearly all the "head ganglia" have been subjected to renewed investigation. Van Gehuchten[2] has shown that, when stained with the Golgi method, the Gasserian ganglion and the ganglia on the vagus and glosso-pharyngeal, "are comparable in all points to the spinal ganglia," and Lenhossék[3] that the cells of the geniculate ganglion are of the same type. In the acous-

tic ganglion, when impregnated with chrome silver, bipolar cells were found by Retzius[4], Van Gehuchten[2], Cajal[5], Ayers[6], and Lenhossék[7]. Of the other head ganglia studied with the chrome-silver method, the spheno-palatine (Lenhossék[8]) and the ciliary (Retzius[9]) were found to be sympathetic in nature, containing multipolar cells.

This leaves, then, the submaxillary and the otic as the only ganglia found in connection with the cranial nerves which have not been stained by the Golgi method. It seemed to me desirable, in view of the physiological interest attached to the so-called submaxillary ganglion and the nerves in connection with it, to submit it to more careful study; to determine, if possible, the character of its cells and their relation to incoming and outgoing nerve fibres.

Methods.—Two methods have been used—the double Golgi-Cajal method and the Ehrlich-Bethe methylene-blue method. When using the former, the tissues were placed for three or four days in the osmium-bichromate solution, then in three-quarter-per-cent silver nitrate for three days, again in the osmium-bichromate mixture for two days, and finally for three or four days in a three-quarter-per-cent silver-nitrate solution. They were then hastily dehydrated, embedded in collodion, and cut. The sections were cleared in oil of bergamot and xylol and mounted under cover glasses in Canada balsam. I wish to lay stress on the last-mentioned step, as there seems yet a general belief that when preparations are so mounted they are destined to fade in a short time. This is certainly not the case if after placing the sections on the slide the xylol is thoroughly removed with filter paper, and after covering them with a relatively large amount of balsam, the slide is carefully heated over a flame for one or two minutes, or until so much of the solvent has been driven off that the balsam "sets" as soon as it cools. Before cooling, a warm cover glass is placed over the sections. My experience shows that Golgi sections mounted in this way will keep four years without in the least fading.

The Ehrlich-Bethe method was used in the following way: The fresh tissues were stained for about an hour in a one-per-cent solution of methylene blue in normal salt solution, fixed, as Bethe[10]

recommends, in a solution of ammonium molybdate, embedded in paraffin, cut, and mounted.

The following observations were made on specimens obtained from young dogs, and from puppies varying in age from one to ten days. In each animal I exposed the sublingual and submaxillary glands, their respective ducts, the chorda-lingual nerve and triangle. The chorda-lingual triangle (this term is used after Langley [11] and refers to the triangle of tissue between the lingual nerve, chorda tympani, and submaxillary duct), with the underlying sublingual gland and the oral mucous membrane mesial to it, was excised as one piece; the remaining portion of the submaxillary duct, and a thin segment extending through the entire thickness of the submaxillary gland, embracing its hilum, the primary divisions of Wharton's duct, and such lobular ducts as would fall within the segment, as another piece. The tissues so removed were then treated as above mentioned.

Histological Observations.—It is necessary, in the first place, to state that it is not quite correct to speak of a submaxillary ganglion in the sense now generally used, for, as Langley [11] has shown, there are found in the chorda-lingual triangle quite a large number of groups of ganglion cells; the so-called submaxillary ganglion is only one, perhaps the largest, of this number. This statement I can fully confirm. He further points out that these groups of ganglion cells have no connection with that portion of the chorda tympani which goes to the submaxillary gland. This statement he supports both with histological and physiological data. He suggests that "what has hitherto been called the submaxillary ganglion would more correctly be called the sublingual ganglion," and in speaking of the group of ganglia found in the chorda-lingual triangle I shall adopt this nomenclature.

Langley's [11] observations as to the ganglia found in connection with the submaxillary gland are as follows: "Very soon after the submaxillary duct has run free from the sublingual, nerve cells are found upon the medullated bundles which accompany it. The nerve cells are in greater number and form a ganglion much larger

than the so-called submaxillary ganglion." And again: "It is well known that nerve cells occur here and there in the course of the nerve fibres round the lobular duct." I gather, from an examination of preparations made from a large number of glands, that several fairly large groups of ganglion cells are found in connection with the chorda tympani (as it follows Wharton's duct) at a point where it is about to enter and just after it enters the gland, smaller groups being in connection with such of its branches as enter the gland and accompany the larger gland ducts. These observatons verify in the main those quoted from Langley. When necessary to make mention of this group of ganglia, it will be referred to as the submaxillary ganglion.

In all preparations stained after the Golgi method in which the impregnation was successful the nerve cells of the sublingual and the submaxillary ganglia are multipolar in type. As may be seen from Plate XI, Fig. 1, which is a reproduction of the cells stained in one of the smaller ganglia found in the submaxillary gland, the processes are given off largely from one side of an oval or round body. They are usually quite short, often dividing into two or three secondary branches which interlace with similar processes from other cells. It is not unusual, however, to find here and there a cell (Plate XI, Fig. 1, *a*) from which a process is given off, which can be traced for a longer or shorter distance in the field, and which, when viewed a short distance from the cell, is, as a rule, beset with varicose enlargements and does not branch. There can be no doubt that we are here dealing with the axis-cylinder process, while the others may be looked upon as protoplasmic branches. The cells of the sublingual ganglion present the same appearance.

A comparison of the cells here sketched and described—with the descriptions and diagrams of sympathetic cells, found in the reports of investigators, who have in recent years turned their attention to the study of the sympathetic system with the Golgi method—will show that the cells of the sublingual and the submaxillary ganglia are sympathetic in nature, the reports of Kölliker [12], Cajal [13], Van Gehuchten [14], Retzius [15], Sala [16], and Lenhossék [8] showing that

sympathetic cells are multipolar, with one unbranched axis-cylinder process.

Mention may here be made that Retzius[17] has described and diagrammed small groups of sympathetic ganglion cells found by the side of the larger ducts and blood vessels of the submaxillary gland. He was not, however, able to determine the fate of their processes.

The question may now be asked, What is the distribution of the axis-cylinder processes of the sympathetic cells of the sublingual and submaxillary ganglia? The account gathered from an examination of preparations made from submaxillary glands stained after the Golgi method will here be presented; the conditions here are somewhat simpler, as many of the groups of ganglion cells belonging to the submaxillary ganglion are found in the gland itself, which is not the case for the sublingual gland and ganglion. The small groups of ganglion cells are found in the immediate neighbourhood of the lobar and lobular ducts; I have not found any on the walls of the vessels. From such a ganglion small bundles of thin nerve fibres, many of which are varicose and into which one can now and then trace the axis cylinder of a sympathetic cell of the ganglion, can be followed for a longer or shorter distance along the side of the duct on which the ganglion is situated. In successive sections of a series, small bundles will be found accompanying the ducts, and these or similar bundles can be traced further and further into the lobules of the gland. About the intralobular ducts, especially the smaller ones, there is found a toleraby dense plexus of fine nerve fibres. From the plexus strands of two, three, or more fibres, or single fibres, are given off, and can be followed between the alveoli, where they unite to form a perialveolar or epilamellar (Arnstein) plexus (Plate XI, Fig. 2). It seems superfluous to state that the ducts of a gland like the one under discussion branch in such a way that it is quite out of the question to cut sections any single one of which contains a portion of the submaxillary duct, one or several of its primary branches, and even one of the intralobular ducts, with its system of end branches and alveoli. When, in addition to this, the precariousness of the Golgi method is taken into consideration, one would hardly expect to find

sections in which the sympathetic cells were successfully stained, the axis cylinders of which can be followed along the larger and smaller ducts to their ultimate distribution about the alveoli. In a few instances, however, an axis cylinder from a sympathetic cell, which was observed accompanying a duct for a short distance, could be followed as it left the duct and approached a group of alveoli; and in one instance, in a section of the chorda-lingual triangle, which also contained a portion of the sublingual gland, two sympathetic cells deeply stained were seen, the axis cylinder of one of which could be followed for quite a distance by the side of an intralobular duct, and after a short interruption a fibre of the same size and appearance could be traced into a perialveolar plexus. I am well aware that the account here presented is fragmentary; the instance last mentioned seemed, however, so conclusive that I feel justified in stating that the axis cylinders of the sympathetic cells accompany the ducts and ultimately form a plexus about the alveoli.

Retzius described in 1888 a plexus of fine fibrillæ about the alveoli of the "small salivary glands" found in the tongue of a rabbit near the papilla foliata. These observations were made on preparations stained in methylene blue. The following year Ramón y Cajal[18], in a brief notice on the ending of the nerves in the salivary glands, gave the results as obtained with the Golgi method. He here states that "in the submaxillary gland of the rat and rabbit the nerve fibres are arranged in the form of a plexus with round or polygonal meshes. The bundles of this plexus differ in thickness, often have a wavy course, and are composed of non-medullated axis cylinders varying in size. The axis cylinders divide during their course, and give off fine varicose fibrillæ which seem to end on the membrana propria or on the outer surface of the cells." Retzius[17], in a later publication on the basis of renewed investigation with the chrome-silver method, states that he is able to verify in full his earlier observations, and confirms the results obtained by Cajal. Regarding the ultimate distribution of the fibres of the perialveolar plexus and their relation to the cells of the alveoli there is as yet a divergence of opinion. Retzius[17] states that "he was unable to

determine whether the nerve fibres terminated on the outer surface of the membrana propria or between it and the gland cells; certain it is that they end very near the gland cells, and it is very probable that they come in direct contact with them." Cajal, as above quoted, traces the ultimate fibrillæ to the outer surface of the salivary cells.

Arnstein[19] has recently reported on some work which he and his pupils have been carrying on with the methylene-blue method. He himself has investigated the pancreas, the salivary and Harder's glands, Timofeew the prostate, Ostroumow the skin glands, and Dmitrewsky the mammary gland. In a *résumé* Arnstein expresses himself as follows: "In all tubular and acinous glands one finds an epilamellar network which lies on the membrana propria; from this fine fibres are given off which pass through the membrana and, as pericellular threads, come in contact with the gland cells. These fibres form no network under the membrana; they may divide, and end in varicose filaments, the configuration of which differs in different cells."

In some of my preparations, in which the perialveolar plexus was well stained with chrome silver, I now and then find very fine varicose fibrillæ given off from it. They often present a very irregular course, now and then are seen branching, and seem to end on or between the gland cells. They lie in a plane a little deeper than the perialveolar plexus, are much finer than its fibres, and more often show a beaded appearance. As far as my observation goes, these ultimate fibrillæ, which seem to correspond to the pericellular branches which Arnstein[19] and his pupils find below the membrana propria, end in very small nodules or granules. I have not seen the more complicated ending described by Arnstein.

The facts gathered from the literature reviewed, and the observations made by myself, may be expressed in the following brief summary: The axis-cylinder branches of the sympathetic cells found by the side of the ducts of the submaxillary gland are grouped into small bundles which accompany the branches of the ducts to the lobules and here form a plexus about the intralobular duct, from which branches are in turn given off which form a second plexus on

the membrana propria about the alveoli; from this plexus fibrillæ penetrate the membrana propria and end on the gland cells.

We may now turn to the chorda tympani. Langley [11] has shown that "it consists of four or five small bundles of medullated nerves. . . . Besides these, several other small bundles of fine medullated fibres are given off by the lingual in its course between the point where it gives off the chorda tympani proper and where it crosses the duct of the submaxillary gland. These bundles are given off from both sides of the lingual nerve; after a very short course, nerve cells occur within the sheath of the nerve bundles; the nerve cells are scattered among, though often collected chiefly on one side of, the medullated nerve fibres; on the distal side of the nerve cells non-medullated fibres are found, and the medullated fibres are reduced in number." And again, after describing the location of the ganglion cells in the hilum of the submaxillary gland, as previously quoted, he states that "from the distal end of this (submaxillary ganglion) issue bundles which contain comparatively few medullated fibres." The non-medullated fibres issuing from the distal portion of the groups of ganglion cells of sublingual and submaxillary ganglia are no doubt the axis-cylinder processes of the sympathetic ganglion cells of the several ganglia, concerning which mention has above been made.

In some of the Golgi-stained preparations made from the chorda-lingual triangle and submaxillary gland, in which the ganglion cells are not at all or only imperfectly stained, and in others stained in methylene blue, I find a very dense plexus of fine varicose fibrillæ surrounding the ganglion cells. This plexus is woven into a basket-like structure, and into it one can at times trace a rather coarse axis cylinder. This pericellular network I have found a great number of times, and in various ganglia of the sublingual and submaxillary group.

In methylene-blue preparations the fibrillæ of the plexus are of a violet-blue colour, on which more deeply stained granules are discernible. The inclosed ganglion cell, with its processes, either remains unstained, or only the cell body and nucleus are tinged a very light blue.

In Golgi-stained preparations this plexus is not seen when the cells are stained. In some of the preparations in which the cells remained unimpregnated beautiful examples were found. The shape and arrangement of this basketlike network was essentially the same in methylene-blue and chrome-silver preparations, except that in the latter case the fibrillæ appeared somewhat coarser. One such pericellular basket is reproduced in Plate XI, Fig. 3; it was taken from one of the small ganglia of the submaxillary gland in a preparation stained after the Golgi method. A rather coarse axis cylinder can with some difficulty be followed between some other stained fibres, and, as the figure shows, divides into a number of branches (at *b*), which, after further branching, anastomose to form the network.

Does this pericellular network indicate the ending of the nerve fibres of the chorda tympani? The following reasons suggest themselves for assuming that it does:

1. Langley[11] has shown that medullated fibres approach the ganglia and a great number of non-medullated fibres are given off from their distal end.

2. In cases where it was possible to determine the direction of an axis cylinder ending in a pericellular network its course was toward the centre.

3. Axis cylinders terminating in a pericellular network are usually somewhat coarser than the axis-cylinder processes of sympathetic cells which are often found beside them; their course is more regular, and in methylene-blue preparations I have a few times recognised the presence of a sheath of myelin at a short distance from their termination in a pericellular network.

4. It is a well-known fact in physiology that stimulation of the chorda-tympani causes an increased flow of saliva. Langley and Dickinson have shown that "nicotine in moderate doses paralyzes the nerve cells in sympathetic ganglia without paralyzing the peripheral ending of nerve fibres." Langley[11] finds that "when a certain amount of nicotine is injected into the vein of a cat, or of a dog, stimulation of the chorda-lingual nerve causes no secretion"; this, as he states, has also been observed by Heidenhain. If, how-

ever, the electrodes are pressed into the hilum of the submaxillary gland and strong tetanizing shocks are used, a secretion nearly as rapid, as when the chorda lingual is stimulated before the injection of nicotine, is obtained. He further shows that the flow of saliva is not due to stimulation of the sympathetic nerves about the submaxillary artery, as after the injection of atropine in sufficient quantity to paralyze the chorda, but insufficient to paralyze the sympathetic, stimulation at the hilum of the gland gives little or no flow. From this Langley concludes that "nicotine paralyzes the nerve cells on the course of the chorda-tympani fibres."

In methylene-blue-stained preparations axis cylinders can often be traced through a ganglion without terminating in a pericellular end-basket. They no doubt are the few medullated fibres which, in conjunction with non-medullated fibres, issue from the distal portion of ganglia. We may assume that such medullated fibres end in pericellular networks in more distant ganglia, as among the fibres composing the network about the intralobular ducts no medullated fibres are seen.

It would seem that now and then the axis cylinder of a medullated fibre branches and forms a network about more than one cell. I have seen one example where an axis cylinder divided into two branches, each of which terminated in a pericellular network.

That there exists a network of fine nerve fibres about sympathetic cells is now well known, and has been shown by a number of investigators. In Ehrlich's [20] first publication concerning the reaction of methylene blue on living nerve tissue he speaks of the sympathetic cells (presumably in the frog) as bipolar, with a straight and a spiral process. In his preparations only the spiral process was stained. This he describes as dividing and forming a network which wholly or partially incloses the cell body. From this network fine fibrillæ were given off which terminated on the cell in small enlargements. Two years later Smirnow [21] published his observations on the structure of sympathetic cells of amphibia. The sympathetic chain and the cells found in the pharynx, lung, septum auriculi, and bladder of frogs and toads were investigated. His results were in the main con-

firmatory of those obtained by Ehrlich, with this exception: that he was not able to see the free ending of fibrillæ given off from the pericellular network, as described by the originator of the methylene-blue method. After discussing at some length the nature and course of axis cylinders ending in the network, Smirnow [21] makes the following statement, which I quote in full:

"*Auf Grund der eben mitgetheilten Thatsachen gelange ich zu dem Schluss, dass die Spiralfasern gegen die Peripherie hinziehen und dass sie Nervenfibrillen enthalten, welche letzere je nach dem Fundort der Nervenzellen zu verschiedenen peripheren Gebilden in Beziehung treten.*"

That these conclusions are erroneous is shown, I think, in what has already been said in giving the reason for believing that the pericellular network about the sympathetic cells of the sublingual and submaxillary ganglia are the terminal endings of the chorda tympani. As there stated, the fibres ending in the baskets extend centralward and are not distributed peripheral to the ganglia. Aronson [22] has described a similar pericellular network about the sympathetic cells of the neck, and the abdominal and cardiac ganglia of the rabbit; and Timofeew [23] about the ganglion cells found in the epididymis.

Lenhossék [8] describes and pictures one very typical pericellular basket seen in the spheno-palatine ganglion of a newborn mouse treated with chrome silver; he adds that the nerve fibre could be followed only a short distance and extended centralward. Lenhossék also describes free ending of nerves in sympathetic ganglia. Whether this is the case in the submaxillary and sublingual ganglia I can not say, as I am unable to state whether the fine fibrillæ found between ganglion cells are to be interpreted as a free ending or as imperfectly stained end-baskets.

Sympathetic Fibres accompanying the Gland Artery.—It is a well-known fact that sympathetic nerve fibres accompany the submaxillary artery to the gland. Langley [11] has shown that "up to the distal end of the ganglion in the hilum—that is, the real submaxillary ganglion—they are unconnected with the plexus resulting

from the chorda tympani, and have no nerve cells on it. This gives ground for concluding that sympathetic nerve fibres are not connected with nerve cells which occur in the course of the chorda tympani." Langley[11] has also shown that when sympathetic cells are paralyzed by the injection of nicotine into the veins of cats, rabbits, and dogs, or after the application of this drug to the superior cervical ganglia, stimulation of the sympathetic in the neck causes no secretion, but that a secretion is obtained when the ganglion or the nerve fibres coming from it are stimulated. He concludes that "the secretory fibres of the sympathetic are not connected with nerve cells beyond the superior cervical ganglion."

The following observations were made on preparations stained in methylene blue and in chrome silver:

Fine varicose fibres, woven into a plexus, were found on the walls of vessels in submaxillary and sublingual glands. Ganglion cells in connection with such fibres have not been observed; neither could they be traced into ganglia found on gland ducts (submaxillary gland); nor were they observed ending near gland cells. These statements would confirm the results obtained by Langley. On putting these facts together, I conclude that the sympathetic fibres going to the sublingual and submaxillary gland with the gland arteries end on the vessels.

One other observation may here receive brief mention—namely, the ending of nerve fibres in the submaxillary and sublingual ducts. These ducts are surrounded by a loose plexus composed of small bundles of nerve fibres. From the plexus axis cylinders are given off which, after repeated division, approach the epithelium, ending therein in very fine varicose fibrillæ.

Plate XI, Fig. 4, shows such an ending in the submaxillary duct. It was taken from a preparation stained in methylene blue. As may be seen from the figure, the ultimate fibrillæ end between the cells of the epithelium. The intra-epithelial branches are usually quite straight, end in small enlargements, and often extend to very near the free ends of the cells between which they are found.

Plate XI, Fig. 5, expresses by way of diagram the general con-

clusions reached. It is based on observations here recorded and on facts gathered from Langley's admirable paper on "salivary secretion," from which I have so largely drawn.

The sublingual and submaxillary ganglia are groups of sympathetic ganglion cells (f, g). The axis cylinders of these cells (f', g') follow the ducts to the glands and end on the cells of the alveoli (a and b). The chorda tympani (d) contains fibres, some of which (d') end in the sublingual ganglion, others (d'') in the submaxillary ganglion. In both ganglia the fibres of the chorda tympani terminate in a pericellular network which incloses the sympathetic cells. The fibres of the chorda tympani going to the submaxillary ganglion have no connection with the nerve cells in the chorda-lingual triangle (e, e', e'').

The sympathetic fibres (h') which accompany the gland arteries are axis cylinders of sympathetic ganglion cells situated in the superior cervical ganglion (h). They end on the blood vessels (k, k') of the glands.

Addendum.—After this article was in the hands of the publishers my attention was called to Berkley's * studies of the nerve endings in the submaxillary gland of the mouse.

Berkley's preparations were obtained from tissues stained in chrome silver, prefixed in picric acid. In the main, Berkley's results receive confirmation in the observations recorded by me. The entrance of the nerve fibres with the blood vessels and ducts, the plexus around the ducts, the meshwork and single fibres about the alveoli (perialveolar plexus), and the ending on or between the gland cells, have received essentially the same interpretation.

In the hilum of the gland, "and located near a secretory duct and an artery," Berkley finds "nests of large unstained sympathetic cells." In none of my sections did I ever find ganglion cells in conjunction with the blood vessels, only on the gland ducts, nor was I able to trace any nerve fibres from the ganglia to the blood vessels, as

* The Intrinsic Nerves of the Submaxillary Gland of Mus Musculus. *The Johns Hopkins Hospital Reports*, vol. iv.

he describes. In all preparations where nerve cells and axis cylinders were well stained the axis cylinder was seen accompanying the ducts.

Berkley makes no mention of the pericellular baskets (endings of the chorda tympani) to which especial attention has been drawn in this article.

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FIG. 1

FIG. 2.

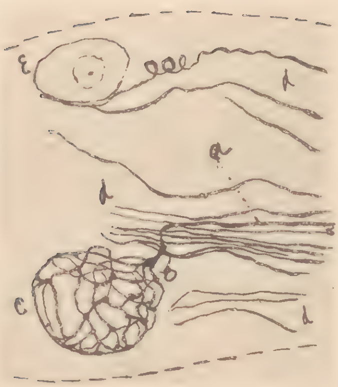

FIG. 3.

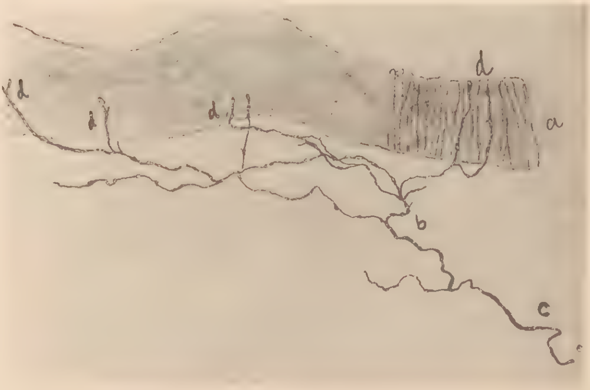

FIG. 4.

FIG. 5.

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Description of Figures, Plate XI.

Fig. 1.—Sympathetic ganglion cells in Golgi-stained preparation. One of the small ganglia in submaxillary gland; *a*, cells showing a well-stained axis-cylinder process; *b*, medullated nerve fibres entering ganglion.

Fig. 2.—To show intralobular duct (*a*) surrounded with a plexus of fine axis cylinders; *b*, alveoli with perialveolar plexus. Golgi stain.

Fig. 3.—To show pericellular end-basket; *a*, coarse axis cylinder branching at *b*; *c*, pericellular end-basket; *e*, unstained ganglion cell; *d*, other axis cylinders. Golgi-stained preparation.

Fig. 4.—To show ending of nerves in epithelium of submaxillary duct; *a*, epithelium lining duct; *c*, axis cylinder branching at *b*, and *d*, intra-epithelial fibrillæ. Methylene-blue stain.

Fig. 5.—Diagram of nerve supply of sublingual and submaxillary glands; *a*, lobules of sublingual gland; *b*, lobules of submaxillary gland; *c*, fibres of lingual nerve; *d*, fibres of chorda tympani; *d′*, chorda-tympani fibres ending in chorda-lingual triangle; *d″*, chorda-tympani fibres ending in submaxillary ganglion; *f*, sympathetic-nerve cells of sublingual ganglion; *f′* their axis-cylinder branches; *g*, cells of submaxillary ganglion; *g′*, their axis-cylinder branches; *h*, cells of superior cervical ganglion; *h′*, axis cylinders; *k*, blood vessels of sublingual gland; *k′*, blood vessels of submaxillary gland.